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Calocidaris micans (Cidaridae) and *Pseudoboletia maculata* (Toxopneustidae): additions to the sea urchin fauna (Echinodermata: Echinoidea) of the Gulf of Mexico

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Abstract.—Two sea urchins (*Calocidaris micans, Pseudoboletia maculata*) were collected and photographed in the Gulf of Mexico between 1978 and 1998. These constitute new records for their distributions. *Calocidaris micans* has been reported previously off the northwestern coast of Cuba, in the Yucatan Channel, and off Barbados. One of our specimens was photographed and collected in the northeastern Gulf of Mexico off Alabama at 100 m. Unpublished museum holdings (USNM) add a second record off Louisiana at 129–144 m. *Pseudoboletia maculata* is distributed in the Pacific Ocean from Ceylon to Japan, in the South Atlantic only at Ascension and St. Helena islands, and in the North Atlantic from Venezuela, Barbados, and off the Atlantic coast of the United States from Florida to North Carolina. An unpublished document of a federal agency reported this sea urchin from the western Gulf of Mexico. Our collections and photographs from off Pensacola, Florida, at ca. 40 m depth revealed that *P. maculata* occurs there in mixed-species aggregations with the echinoid *Lytechinus variegatus*. These records bring the echinoid fauna of the Gulf of Mexico to 61 species, only one of which is endemic and 39 of which have West Indian-Caribbean distributions. Although these records probably are not range extensions within recorded human history, they might represent a post-glacial (re)invasion of the Gulf of Mexico within the last 9000 yr as patchily distributed live-bottom biotopes at intermediate depths became available. These depths and biotopes—poorly sampled in the past—have become more accessible for survey using current sampling technology.

In his review of the echinoid fauna of the Gulf of Mexico, Serafy (1979) listed 89 species, an increase of 23 species from Clark's (1954) list. Serafy pointed out that many of Clark's species are not part of the Gulf fauna proper but have been collected only on its periphery, belonging instead to faunas of the Caribbean, Bahamas, eastern Florida, and the Florida Keys; Serafy's list is annotated to reflect the species restricted to adjacent waters. Apparent inconsistencies in Serafy's two tabulated lists give 53–57 species of echinoid in the Gulf of Mexico proper: *Cidaris abyssicola* (Cidaridae), *Araeolampas atlantica* (Echinothuridae), and *Pourtalesia miranda* (Pourtalesiidae) are not marked as peripheral species, although their distributions would make them so by his criteria; *Echinometra viridis* is listed only as peripheral in his table 1 perhaps by lapsus because Serafy recorded it later in table 2 from several regions within the Gulf. Hulings's (1955) report of *E. viridis* from the northwestern Gulf of Mexico confirmed the presence of this species, although Pomory (2002) does not list it from

the Texas coast. If, then, some interpretation is allowed, the known echinoid fauna of the Gulf stands at 54 species based on Serafy (1979), although numerous misidentifications reported by Turner & Norlund (1988) are cause to question Gulf records of *Brissopsis elongata.*

Defenbaugh (1976) identified specimens of *Echinocardium* from the northern Gulf of Mexico as the European species *E. cordatum* and *E. flavescens* rather than as *E. laevigaster* reported by Clark (1954) and Serafy (1979). Harry (1979) believed that Defenbaugh's specimens were misidentified. Serafy (1979) did not list the toxopneustid *Pseudoboletia maculata,* which was recorded by Pawson (1978) from southeastern Florida and listed and illustrated from the western Gulf of Mexico (Texas A&M University 1981). The reanalysis of *Mellita quinquiesperforata* by Harold & Telford (1990) resulted in its restriction as a western Gulf species and in the elevation of *M. quinquiesperforata tenuis* to species in the eastern Gulf. Hopkins et al. (1991) added *Tretocidaris bartletti* from the northern Gulf off the coast of Alabama; this species was one of Serafy's (1979) peripheral species. Most recently, the record of *Cidaris abyssicola* off the northern coast of the Yucatan Peninsula by Barbosa-Ledesma et al. (2000) places this echinoid well within the boundaries of the Gulf; and these authors also found *Cidaris rugosa* off the western coast of the Yucatan Peninsula and *Stereocidaris ingolfiana* off the northern coast.

In the present report, we confirm *Pseudoboletia maculata* as a part of the Gulf echinoid fauna with the find of a dense aggregation off western Florida, and we add *Calocidaris micans* from one specimen off Alabama and a second off Louisiana. These additions bring to 61 the echinoid species recorded from the Gulf of Mexico.

Materials and Methods

Sea urchins were obtained for this study from Continental Shelf Associates, Inc., Jupiter, Florida, U.S.A., under contract with the U.S. Department of the Interior, Minerals Management Service (*Calocidaris micans*) (Continental Shelf Associates, Inc., & Texas A&M University 2001) and with Chevron U.S.A., Inc., New Orleans, Louisiana (*Pseudoboletia maculata*) (Continental Shelf Associates, Inc. 1996a, 1996b); from the Texas Cooperative Wildlife Collection of Texas A&M University (TAMU); and from the National Museum of Natural History (USNM) of the Smithsonian Institution. Details of collecting localities are given under descriptions of the material. Other records for the Western Atlantic Ocean are based on holdings of USNM, Museum of Comparative Zoology (MCZ) of Harvard University, Harbor Branch Oceanographic Museum (HBOM) of Harbor Branch Oceanographic Institution, California Academy of Sciences, and the Museum of Natural History (BMNH) in London. In most cases, the specimens were examined by us.

Calocidaris micans was collected off Louisiana, U.S.A., with the manipulator arm of R/V *Johnson-Sea-Link I* submersible operated by HBOI in 1989. R/V *Edwin Link* served as the tender.

The R/V *Tommy Munro* served as the tender during survey photography and specimen collection of *C. micans* off Alabama, U.S.A., in 1998. Photographic data and the voucher specimen were collected using a Benthos® open frame SeaROVER remotely operated vehicle (ROV) equipped with color-imaging scanning sonar, manipulator arm, video and 35-mm still cameras, quartz-halogen lamps, and a strobe. The Photosea® underwater still camera and strobe were triggered manually by the onboard scientist. The voucher specimen of *C. micans* was collected using the ROV manipulator arm.

Pseudoboletia maculata was photographed and collected from the East Flower Garden Bank in the NW Gulf of Mexico by Texas A&M University in 1978. The submersible DRV *Diaphus* was equipped with

video and still cameras, a manipulator arm, sediment scoop, and suction sampler (Texas A&M University 1981).

The M/V *Mr. Offshore* was used during survey operations by Continental Shelf Associates, Inc., off Pensacola, Florida, U.S.A., in 1992 and 1993. *Pseudoboletia maculata* was photographed from a towed multicamera system with both video and 35-mm still cameras. Still photographs were taken with a Benthos® 1000 underwater camera and strobe. Specimens were collected by a 7.5-m semi-balloon "mongoose" trawl.

Results

Order Cidaroida Claus, 1880
Family Cidaridae Gray, 1825
Genus *Calocidaris* H. L. Clark, 1907
Calocidaris micans (Mortensen, 1903)
(Figs. 1–2)

Porocidaris sharreri Agassiz, 1880:71 (part.).

Dorocidaris micans Mortensen, 1903:23 (original description), 28 (list).

Calocidaris micans: Mortensen, 1928:312–314 (for complete synonymy, key, description), text-fig. 19-2.—Clark, 1954: 374 (list).—Fell, 1966:U333 (diagnosis).—Phelan, 1970:7–9 (key, description), text-fig. 2, pls. 2, 3.—Serafy, 1979: 10, 14, 109 (key, geographic and bathymetric distributions).

Non-*Calocidaris micans*: Downey, 1968:62 (see note in Phelan 1970:16).

Material examined.—Gulf of Mexico: USNM E47929, 1 spec., dry, 65/76 mm test height/test diameter (TH/TD), R/V *Edwin Link,* R/V *Johnson-Sea-Link I,* dive 2585, Green Canyon, off Louisiana, U.S.A., 27°44′37″N, 91°7′54″W, 129–144 m, 5 Sep 1989; USNM 1002220, 1 spec., alcoholic, 58/73 mm TH/TD, R/V *Tommy Munro* and remotely operated vehicle, Continental Shelf Associates, Inc., job 1600, cruise 3, site 4, sample 335, off Alabama, U.S.A., 29°19′39″N, 87°46′7.8″W, 100 m, manipulator arm, 28 Aug 1998.—Western Atlantic Ocean: MCZ 283, 1 spec., dry, 41/58 mm TH/TD, USCSS *Blake,* sta. 297, off Barbados, 123 fm [225 m], 1879; USNM 10705, 1 spec., alcoholic, 28 mm TD, R/V *Albatross,* sta. 2348, Straits of Florida, off Havana, Cuba, 23°10′39″N, 82°20′21″W, 211 fm [386 m], 20 Jan 1885; USNM 10717, 2 spec., dry and alcoholic, 48 mm TD (dry), 50 mm TD (alcoholic), R/V *Albatross,* sta. 2354, Yucatan Channel, off Cozumel Island, Mexico, 20°59′30″N, 86°23′45″W, 130 fm [238 m], 22 Jan 1885; MCZ 7720, 1 spec., dry, 41/58 mm TH/TD, R/V *Atlantis,* sta. 3305, off Playa Baracoa, Havana Province, Cuba, 330 fm [604 m], 23 Mar 1939; USNM E13068, 1 spec., dry, 77 mm TD, R/V *Gerda,* cruise 6433 (30th biological cruise), sta. 388, NW corner of Little Bahama Bank, Bahamas, 27°18′0″N, 79°12′0″W, 320 m, 19 Sep 1964; USNM E13069, 2 of 3 spec., dry, 53 and 70 mm TD, R/V *Gerda,* cruise 6717, sta. 899, Arrowsmith Bank, Yucatan Channel, off Yucatan Peninsula, Mexico, 20°57′0″N, 86°34′0″W, 40–165 m [one tag reads "102 m"], 10 Sep 1967; USNM E13025, 1 of 2 spec., dry, 56 mm TD, R/V *Pillsbury,* cruise 6802, sta. 595, Arrowsmith Bank, Yucatan Channel, off Yucatan Peninsula, Mexico, 21°8′30″N, 86°27′0″W, 33–586 m, 15 Mar 1968; USNM E13067, 3+ spec., dry, 17, 34, and 70 mm TD, R/V *Pillsbury,* cruise 7001, sta. 1141, off S coast of Great Inagua Island, Bahamas [one tag reads "Caribbean, nr. Haiti"], 20°52′0″N, 73°14′0″W, 403–458 m, 13 Jan 1970; HBOM 72:307, 1 spec., dry, 37/46 mm TH/TD, R/V *Seward Johnson,* cruise 118, R/V *Johnson-Sea-Link II,* dive 579, W of Nassau Harbor, New Providence, Bahamas, 25°7.1′N, 77°26.1′W, 488 m, manipulator, 30 Mar 1981; HBOM 72:339, 1 spec., alcoholic, 46/58 mm TH/TD, R/V *Johnson-Sea-Link I,* dive 1306, off Wood Cay, N of Grand Bahama Island, Bahamas, 274 m, manipulator, 7 Dec 1982; USNM E32546, 1 spec., dry, 57 mm TD, R/V *Seward Johnson,* cruise 157, R/V *Johnson-Sea-Link I,*

dive 1357, W of Wood Cay, Bahamas, 26°42′36″N, 79°1′42″W, 244–309 m, 14 Jun 1983; USNM E32551, 1 spec., dry, 62 mm TD, R/V *Seward Johnson,* cruise 157, R/V *Johnson-Sea-Link I,* dive 1359, W of Wood Cay, Bahamas, 26°42′48″N, 79°9′30″W, 618–624 m, 15 Jun 1983; USNM E32547, 1 spec., dry, 37 mm TD, R/V *Seward Johnson,* cruise 159, R/V *Johnson-Sea-Link I,* dive 1498, French Bay, San Salvador Island, Bahamas, 23°56′0″N, 74°32′54″W, 436–468 m, 21 Oct 1983; USNM E32550, 1 spec., dry, 50 mm TD, R/V *Seward Johnson,* cruise 159, R/V *Johnson-Sea-Link I,* dive 1500, off Cockburn Town, San Salvador Island, Bahamas, 24°2′48″N, 74°32′30″W, 1600 ft [488 m], 22 Oct 1983; USNM E32548, 1 spec., dry, 34 mm TD, R/V *Seward Johnson,* cruise 159, R/V *Johnson-Sea-Link I,* dive 1506, Bonefish Bay, San Salvador Island, Bahamas, 24°4′42″N, 74°33′6″W, 914 ft [279 m], 25 Oct 1983; USNM E32606, 1 spec., alcoholic, 16 mm TD, R/V *Seward Johnson,* cruise 161, R/V *Johnson-Sea-Link II,* dive 805, off Sandy Point, Great Abaco Island, Bahamas, 25°36′12″N, 76°44′30″W, 473 m, 7 Apr 1984; USNM E32580, 1 spec., dry, 48 mm TD, R/V *Seward Johnson,* cruise 161, R/V *Johnson-Sea-Link II,* dive 807, S of Rock Point, Great Abaco Island, Bahamas, 25°59′30″N, 77°24′6″W, 300 m, 8 Apr 1984; USNM E32511, 1 spec., dry, 73 mm TD, R/V *Seward Johnson,* cruise 161, R/V *Johnson-Sea-Link II,* dive 816, Chub Cay, Berry Islands, Bahamas, 25°23′42″N, 77°54′30″W, 226 m, 14 Apr 1984; HBOM 72:505, 1 spec., dry, 24/34 mm TH/TD, R/V *Seward Johnson,* R/V *Johnson-Sea-Link I,* dive 2001, San Salvador Island, Bahamas, 24°13.6′N, 74°29.5′W, 572 m, manipulator, 21 Apr 1987; HBOM 72:498, 1 spec., dry, 43/54 mm TH/TD, R/V *Seward Johnson,* R/V *Johnson-Sea-Link I,* dive 2007, San Salvador Island, Bahamas, 23°0.7′N, 74°33.0′W, 263 m, manipulator, 24 Apr 1987; HBOM 72:743, 1 spec., dry, 48/63 mm TH/TD, R/V *Seward Johnson,* R/V *Johnson-Sea-Link II,* dive 1738, 2.46 nm off Needham's Point, bearing 044°, Barbados, 200–207 m, manipulator, 20 Apr 1989.

Other sources.—In addition to specimens examined by us, we have relied on station data for *Calocidaris micans* deposited in California Academy of Sciences, HBOM, and BMNH.

Descriptions of stations and material.—The specimen of *C. micans* (USNM E47929) taken off the coast of Louisiana at 129–144 m depth was collected by submersible. The following description of the site is based on notes written by S. D. Cairns (in litt.) during the dive. Bottom temperature was 17°C. The site was a ridge oriented from northwest to southeast with a slope of 45° at least on one side. The slope was partly composed of large, flat, imbricated, calcareous slabs that Cairns compared to plates of deep-reef *Agaricia.* The substratum consisted also of gravel and of rocks of various sizes and shapes. A variety of scleractinian and antipatharian corals were observed or collected (Cairns et al. 1993), including a new species of black coral (Opresko & Cairns 1992). Other material collected were three slit shells, another unspecified gastropod, and a crinoid; collection of *C. micans* was not mentioned in Cairns's field notes.

The specimen at hand had a test diameter (TD) of 76 mm and a test height (TH) of 65 mm, giving the test a high globose shape (TH:TD = 0.86) typical of *C. micans.* All primary spines above the ambitus were broken except one (137 mm long; = 1.8 TD); Phelan (1970) reported that primary spines of *C. micans* can be up to 3 TD, although more commonly they are up to 1.5 TD. In addition to morphology of the test and pedicellariae (Mortensen 1928, Phelan 1970), all primary spines had the smooth porcelaneous surface (Fig. 1B, C) that is unique to this species (Phelan 1970). The spines were free of epizoics. Although cidaroid spines are known to harbor epizoics (Hyman 1955), the spines of most *C. micans*

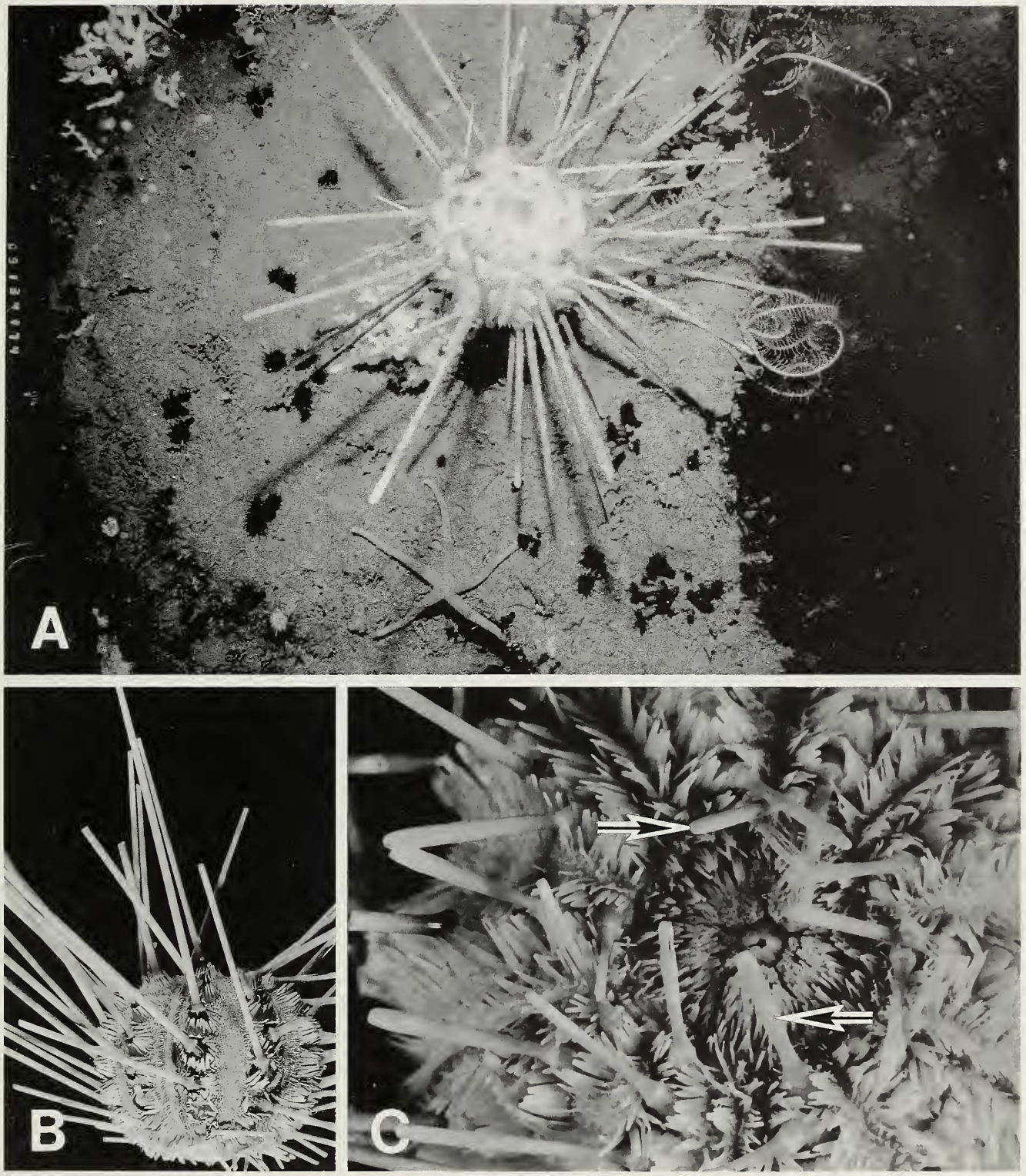

Fig. 1. *Calocidaris micans.* A. USNM 1002220 on ledge at collection site off Alabama, with a colony of the hard coral *Madrepora carolina* to left, the hard coral *Madracis myriaster* to the upper left, two unidentified comatulid crinoids to the right, several individuals of the black ahermatypic coral *Rhizopsammia manuelensis,* and the seastar *Chaetaster nodosus* at the bottom; note epizoics on some of the primary spines of the echinoid; courtesy of Continental Shelf Associates, Jupiter, Florida. B. USNM E47929, showing long, terete, smooth primary spines on ambitus and near apex of test. C. USNM 1002220, oral surface, showing smooth oral primary spines (arrows).

examined by us were rarely covered with epizoics.

The specimen of *C. micans* (USNM 1002220) was photographed and collected off Alabama, U.S.A., at 100 m depth on a high-relief (>2 m) hard-bottom feature described by Ludwick & Walton (1957) as a trend of discontinuous reef-like pinnacles located near the edge of the continental shelf between the Mississippi River delta and DeSoto Canyon. The sampling site was the apex of a relatively large ridge gradually sloping to the west-southwest and to the north. Visually and numerically dominant taxa at the site were hard corals (*Rhizopsammia manuelensis, Madracis myriaster, Madrepora carolina*), soft corals [*Ctenocella* (*Ellisella*) spp., *Nicella* spp.], antipatharians (*Antipathes* spp.), crinoids, basketstars, and various unidentified ahermatypic hard corals.

The in-situ photograph (Fig. 1A) of the specimen at hand showed it on a ledge that was lightly coated with sediment. Associated fauna visible in the photograph were a variety of anthozoans, crinoids, a seastar, and a galatheid crab. Most primary spines at and above the ambitus were broken, and little additional damage was inflicted upon collection of the specimen. The animal in life had pale yellow interambulacra and paler ambulacra, scrobicular spines, and regenerating primary spines. The primary spines otherwise were medium brown, much darker basally, and largely unbanded. Many primary spines of the live specimen exhibited a fuzzy coating, presumably of epizoics; but the only obvious epizoics on the alcoholic specimen were occasional patches of the foraminiferan *Homotrema rubra.* Among other *C. micans* examined, one specimen from Barbados (HBOM 72:743) had spines with barnacles and tubicolous polychaetes. The test of the specimen from Alabama was globose (TH:TD = 0.79).

Remarks.—Calocidaris micans was first collected off Barbados (Fig. 2) at 225 m depth by USCSS *Blake* in 1879 and was one of three specimens in Agassiz's (1880) type material of *Porocidaris sharreri.* [It was not collected again off Barbados for 110 yr when one specimen (HBOM 72:743) was collected by T. Askew at a depth of 200–207 m.] In 1885, R/V *Albatross* took two specimens each from the Straits of Florida (337–386 m) and the Yucatan Channel (238 m). One specimen from the Straits of Florida (NHM 1898.5.3.583) is Mortensen's (1903) holotype of *Dorocidaris micans.* It was in his report on echinoids of the Danish Ingolf Expedition that Mortensen (1903) pointed out Agassiz's (1880) error. Clark (1907:211) erected *Calocidaris* for *D. micans,* naming it presumably because it was "the most beautiful echinoid I have ever seen," an evaluation with which Mortensen (1910) later concurred. Clark (1907) characterized his new genus partly by the smooth, highly polished, porcelain-like primary spines (Fig. 1B) and by the absence of serrations (spinules) even on the oral primaries (Fig. 1C). Phelan (1970) viewed the morphology of the primary spines as diagnostic of *Calocidaris,* pointing out that all other cidaroids have serrations on at least some primaries. Although Clark (1925) later synonymized his *Calocidaris* with *Cidaris,* Mortensen (1928) retained *Calocidaris,* as have echinoid systematists since then. The genus remained monotypic and Recent until Cutress (1980) described *Calocidaris palmeri* from the Middle Miocene of Cuba; Cutress (1980) considered *C. micans* to have descended directly from *C. palmeri* in a process paralleled in *Cidaris* and *Tretocidaris.* For decades, the few specimens of *C. micans* were known only from the Greater and Lesser Antilles.

The cruises of R/V *Gerda* and *Pillsbury* in 1964–1970 collected more specimens from the Yucatan Channel (33–586 m) but added the Bahamas (320–458 m) to its distribution (Fig. 2). Many Bahamian specimens were collected during cruises of R/V *Seward Johnson* and R/V *Edwin Link* using the *Johnson-Sea-Link* submersibles in 1981–1998 at depths of 226–624 m. Not until 1989, 110 yr after its original discovery off Barbados, was *C. micans* taken from

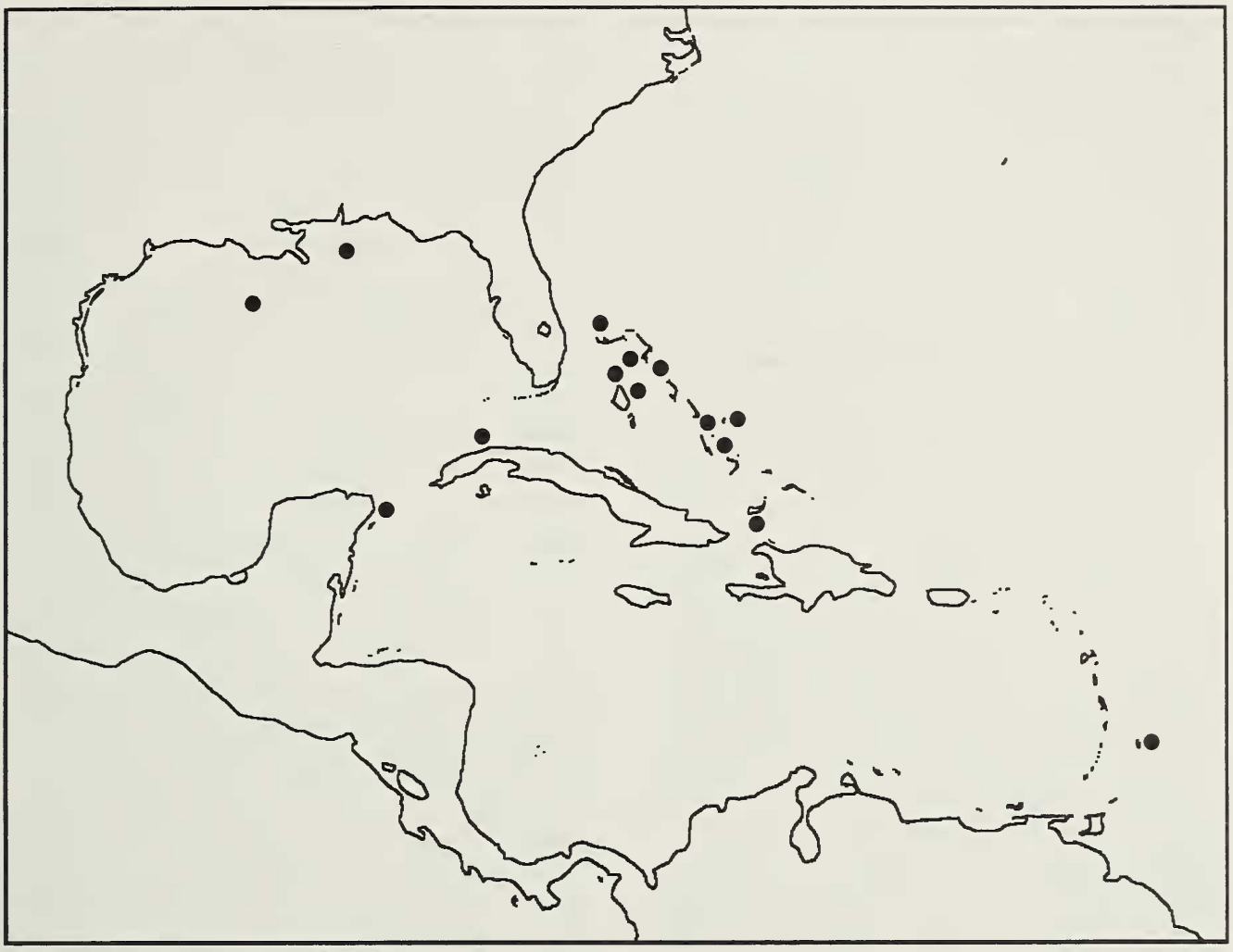

Fig. 2. Distribution of *Calocidaris micans* based on museum records and literature. Each plot might represent multiple nearby records.

the Gulf of Mexico, off Louisiana at a depth of 129–144 m. The second Gulf specimen was photographed in situ (Fig. 1A) and collected in 1998 off Alabama at 100 m. Both specimens were from the northern Gulf of Mexico, well within Serafy's (1979) criteria for inclusion; they are among the largest (73 and 76 mm TD) known specimens of *C. micans* and from among the shallowest stations (<150 m).

Order Temnopleuroida Mortensen, 1942
Family Toxopneustidae Troschel, 1872
Genus *Pseudoboletia* Troschel, 1869
Pseudoboletia maculata Troschel, 1869
(Figs. 3–5)

Pseudoboletia maculata Troschel, 1869:96 (original description).

Pseudoboletia atlantica Clark, 1912:344 (original description), 345 (key).

Pseudoboletia occidentalis Clark, 1921: 115–118, pl. II (original description).

Pseudoboletia maculata: Mortensen, 1943: 528 (key), 532–534 (for complete synonymy, description), pl. XLII, figs. 4, 5; pl. LV, figs. 2, 5, 6, 16, 17, 21.—Pawson, 1978:3–5 (listed), 7 (description), 17–20 (description).—Continental Shelf Associates, Inc., 1979 (station data).—Texas A&M University, 1981:99 (ecology, station data), fig. X-10 (in situ), table X-C-29 (listed).—Duke University Marine Laboratory, 1982:tables 5.9, 5.13, Appendix 20 (listed).—Rowe & Gates, 1995:258 (systematics, distribution).—Continental Shelf Associates, Inc., 1996a:148 (ecology).—Continental Shelf

Associates, Inc., 1996b:15, 17 (ecology), table 1 (listed), pl. B-12.

Pseudoboletia atlantica: Mortensen, 1943: 528 (key), 534–538 (synonymy, description), pl. XXXII, figs. 1–5; pl. XXXIX, fig. 6; pl. XL, fig. 6; pl. XLII, figs. 1–3; pl. XLIII, figs. 1, 2; pl. XLIV, fig. 1; pl. LV, figs. 1, 3, 19, 20.

Pseudoboletia occidentalis: Mortensen, 1943:528 (key); 538–540 (synonymy, description).

?*Lytechinus variegatus*: Continental Shelf Associates, Inc., 1996a:table 5.4 (part., listed).

Material examined.—Gulf of Mexico: TAMU 3-1809, 1 spec., alcoholic, 27/51 mm test height/test diameter (TH/TD), DRV *Diaphus,* cruise 78-G9-D5, dive 5 [night dive], submersible, East Flower Garden, 27°53′N, 93°38′W, 160–190′ [49–58 m], 30 Oct 1978 [one tag reads "9/30/78"]; USNM 1002222, 1 spec., dry, 34/66 mm TH/TD, M/V *Mr. Offshore,* Continental Shelf Associates, Inc., job 1390.3 for Chevron, Destin Dome Unit, survey 2, trawl 22, off Pensacola, Florida, U.S.A., 29°59′N, 87°11′W, 112′ [34 m], 9 Oct 1992; USNM 1002298, 2 spec., dry, 29/58 & 32/65 mm TH/TD, M/V *Mr. Offshore,* Continental Shelf Associates, Inc., job 1390.3 for Chevron, Destin Dome Unit, survey 2, trawl 22, off Pensacola, Florida, U.S.A., 29°59′N, 87°11′W, 112′ [34 m], 9 Oct 1992; USNM 1002299, 1 spec., alcoholic, 42/81 mm TH/TD, M/V *Mr. Offshore,* Continental Shelf Associates, Inc., job 1390.5 for Chevron, Destin Dome Unit, survey 4, trawl 43, sample QSA 2, off Pensacola, Florida, U.S.A., 29°56.25′N, 87°14.3′W, 126′ [38 m], 18 Apr 1993.—Other Atlantic sites: USNM E4531, 1 spec. [holotype of *Pseudoboletia occidentalis* Clark, 1921], dry, 28/54 mm TH/TD, State University of Iowa Barbados-Antigua Expedition, 1918, off Barbados, 30–100 fm [55–183 m], 1918; MCZ 7583, 2 spec., dry, 32/70 & 43/94 mm TH/TD, coll. T. Mortensen, off St. Helena, ca. 15°58′12″S, 5°46′36″W [our estimate from Mortensen (1933)], 50 m, Feb 1930; USNM E5953, 1 spec., dry, 42/89 mm TH/TD, coll. T. Mortensen, off St. Helena, ca. 15°58′12″S, 5°46′36″W [our estimate from Mortensen (1933)], 20 m, Feb 1930; USNM E12353, 4 spec., dry, 31/63–39/79 mm TH/TD, R/V *Pillsbury,* cruise 6806, sta. 736, off Venezuela, 10°57′0″N, 65°52′0″W, 38–85 fm [69–155 m], 22 Jul 1968; USNM E16096, 1 spec., dry [crushed], coll. by "F.M. for A. Loveridge," James Bay, St. Helena, 14 Aug 1968; USNM E11732, 1 spec., dry, 39/82 mm TH/TD, coll. by "F.M. for A. Loveridge," wreck of *Papanui,* James Bay, St. Helena, 1 Feb 1969; USNM E20593, 1 spec., dry, 5.8/12 mm TH/TD, R/V *Pillsbury,* cruise 6907, sta. 878, east of St. Vincent, St. Vincent and the Grenadines [other tags read "off of Saint Lucia" and "off Windward Is"], 13°11′18″N, 61°6′30″W, 37–40 m, 6 Jul 1969; USNM E16204, 1 spec., dry, 39/85 mm TH/TD, coll. Rick Guest, off Hillsboro Beach, Florida, U.S.A., 70′ [21 m], 7 Mar 1974; USNM E16202, 1 spec., dry, 30/60 mm TH/TD, coll. R. Guest, off Hollywood, Florida, U.S.A., 65′ [20 m], spring 1974; USNM E16203, 1 spec., dry, 33/74 mm TH/TD, coll. R. Guest, off Hollywood, Florida, U.S.A., 65′ [20 m], 6 May 1974; USNM E16246, 2 spec. [1 crushed], 33/75 mm TH/TD, coll. M. Telford, Carlisle Bay, Barbados, 40′ [12 m], 1976; HBOM 72:278, 1 spec., dry, 34/74 mm TH/TD, Continental Shelf Associates, Inc., sta. James Island-380, sample 14A-a, Charleston, South Carolina, U.S.A., from 32°34.9′N, 78°34.8′W to 32°35.2′N, 78°35.0′W, 53 m, biological dredge, 2 Oct 1978; USNM E29871, 1 spec., dry, 35/75 mm TH/TD, R/V *Dan Moore,* Living Marine Resources Study, sta. OS05 (field no. 818118), off North Carolina, U.S.A., 33°48′42″N, 76°34′12″W, 102 m, trawl, 14 May 1981; USNM E32267, 2 spec., alcoholic, 73 & 74 mm TD, R/V *Dan Moore,* Living Marine Resources Study, sta. OS05 (field no. 818169), off North Carolina, U.S.A., 33°49′0″N, 79°34′0″W, 69 m [one

tag reads "33°49.1′ 76°34.0′ 66 m"], trawl, 10 Aug 1981; USNM E29626, 1 spec., alcoholic, 68 mm TD, R/V *Dan Moore,* Living Marine Resources Study, sta. OS05 (field no. 818171), off North Carolina, U.S.A., 33°49′30″N, 76°34′0″W, 63 m, trawl, 11 Aug 1981; USNM E30528, 7 spec. [1 crushed], alcoholic, 66–85 mm TD, R/V *Dan Moore,* Living Marine Resources Study, sta. OS05 (field no. 818179), off North Carolina, U.S.A., 33°49′24″N, 76°33′24″W, 68 m, trawl [W. W. Kirby-Smith, in litt.; but museum records indicate "Smith-MacIntyre grab"], 11 Aug 1981.

Other sources.—In addition to specimens examined by us, we have relied on station data for other *Pseudoboletia maculata* deposited in BMNH and HBOM.

Descriptions of stations and material.—*Pseudoboletia maculata* were photographed on and collected from the NW rim of DeSoto Canyon off Pensacola, Florida, in 1992–1993 on a soft substratum that supported a biotal assemblage referred to as a "sand bottom algal community" (Continental Shelf Associates, Inc. 1996a, 1996b). The sand bottom algal community was visually dominated by calcareous red algae (Corallinaceae and *Peyssonnelia inamoena*) and closely associated with coarse substratum consisting of coralline algal rubble, shell debris, and coarse sand. The substratum supporting the sand bottom algal community produced a relatively strong acoustic side-scan sonar reflection, indicating a coarse grain size and relatively high shell content (Marine Technical Services, Inc. 1985; John E. Chance & Associates 1991a, 1991b, 1992).

The presence of abundant algae on the sand substratum in water depths of approximately 30–55 m supported relatively dense aggregations of grazing echinoids (*Astropyga magnifica, Eucidaris tribuloides, Lytechinus variegatus, P. maculata, Stylocidaris affinis*). *Pseudoboletia maculata* was only observed in mixed-species aggregations with the echinoids *Lytechinus variegatus* and *Eucidaris tribuloides* (Fig. 3A). Other biota observed and collected with *P. maculata* included the free-living hard coral *Oculina tenella,* the scallop *Pecten ravenelli,* and rock shrimp *Sicyonia brevirostris.* The algal density within the area exhibited high variability (Continental Shelf Associates, Inc. 1996a) probably due to seasonal changes in light or temperature in combination with other oceanographic conditions. *Peyssonnelia inamoena,* the dominant alga closely associated with the presence of *P. maculata,* has been observed to vary seasonally in density in other areas where it is found (Schneider 1976).

Eight non-overlapping photographs showed 1–18 *P. maculata* per frame, with occasional *Eucidaris tribuloides* and possible *L. variegatus* (Fig. 3A). Many *P. maculata* had debris on their tests. Maculae were not visible in the photographs, but the large size and low hemispherical shape of most of the urchins distinguished them as *P. maculata* rather than *L. variegatus.* Many of the *P. maculata* were clumped, sometimes with spines in contact with neighbor's spines; but, elsewhere, animals were several test diameters apart.

Four *Pseudoboletia maculata,* test diameters 58–81 mm, were collected at two stations 5 nm apart in a sand bottom algal community. The specimens were mixed with *Lytechinus variegatus* (USNM 1002300 and 1002301), which has a proportionately higher test than *P. maculata* (Fig. 4). Only one of the four specimens had maculae (Fig. 3B), which occurred in three cycles: one cycle of pigmented spots subapical in the interambulacra; two cycles of spots, one just above and one just below the ambitus, each cycle consisting of five large interambulacral and five small ambulacral maculae. Each macula was formed by a group of primary and secondary spines, most primary spines dark brown basally, fading to pale green medially and white distally. Otherwise, the spines and test were white. Our observations of spine coloration agree with those of Koehler (1908), Mortensen (1943), and Pawson (1978).

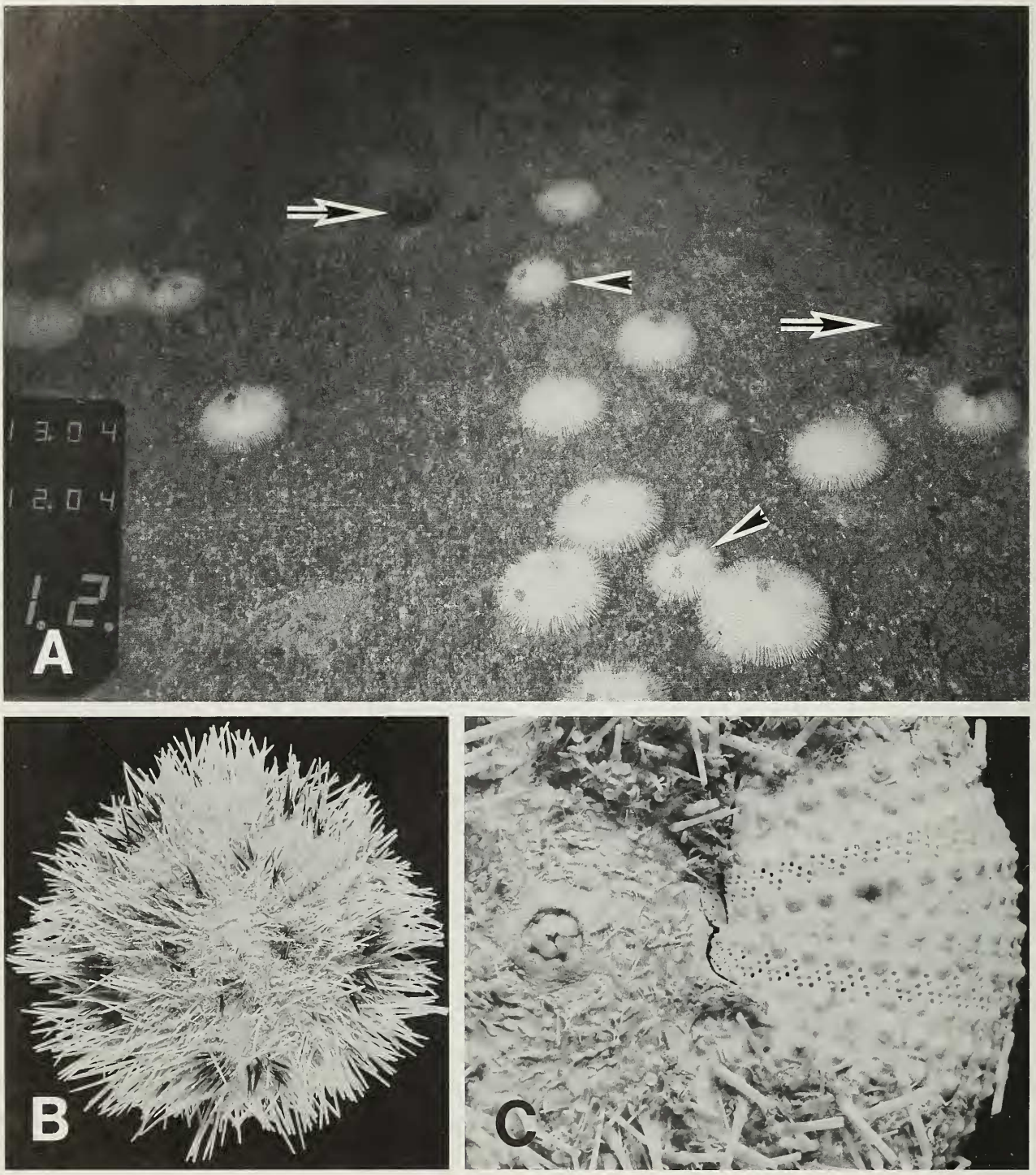

Fig. 3. *Pseudoboletia maculata.* A. Photograph of collection site off Pensacola, Florida, showing an aggregation of *P. maculata* with two possible *Lytechinus variegatus* (arrowheads; based on size and shape) and two *Eucidaris tribuloides* (arrows); courtesy of Continental Shelf Associates, Jupiter, Florida. B. USNM 1002299, specimen from off Pensacola, Florida, showing maculae. C. USNM 1002222, specimen from off Pensacola, Florida, showing pore pairs in arcs of four and spination of plates in the buccal membrane.

In addition to the material off Florida, one specimen (TAMU 3-1809) of *P. maculata* was collected by T. J. Bright in 1978 on a night submersible dive at 49–58 m on the western side of East Flower Garden Bank, a salt dome in the western Gulf of Mexico. The cidaroid *Stylocidaris affinis* was the only other echinoid recorded from the dive (Texas A&M University 1981). Submersible observations revealed high densities of *P. maculata, Arbacia punctulata,* and the asteroid *Linckia nodosa* at 46–76 m, and one photograph taken in 1979 of the sea floor showed 46–50 *P. maculata* on

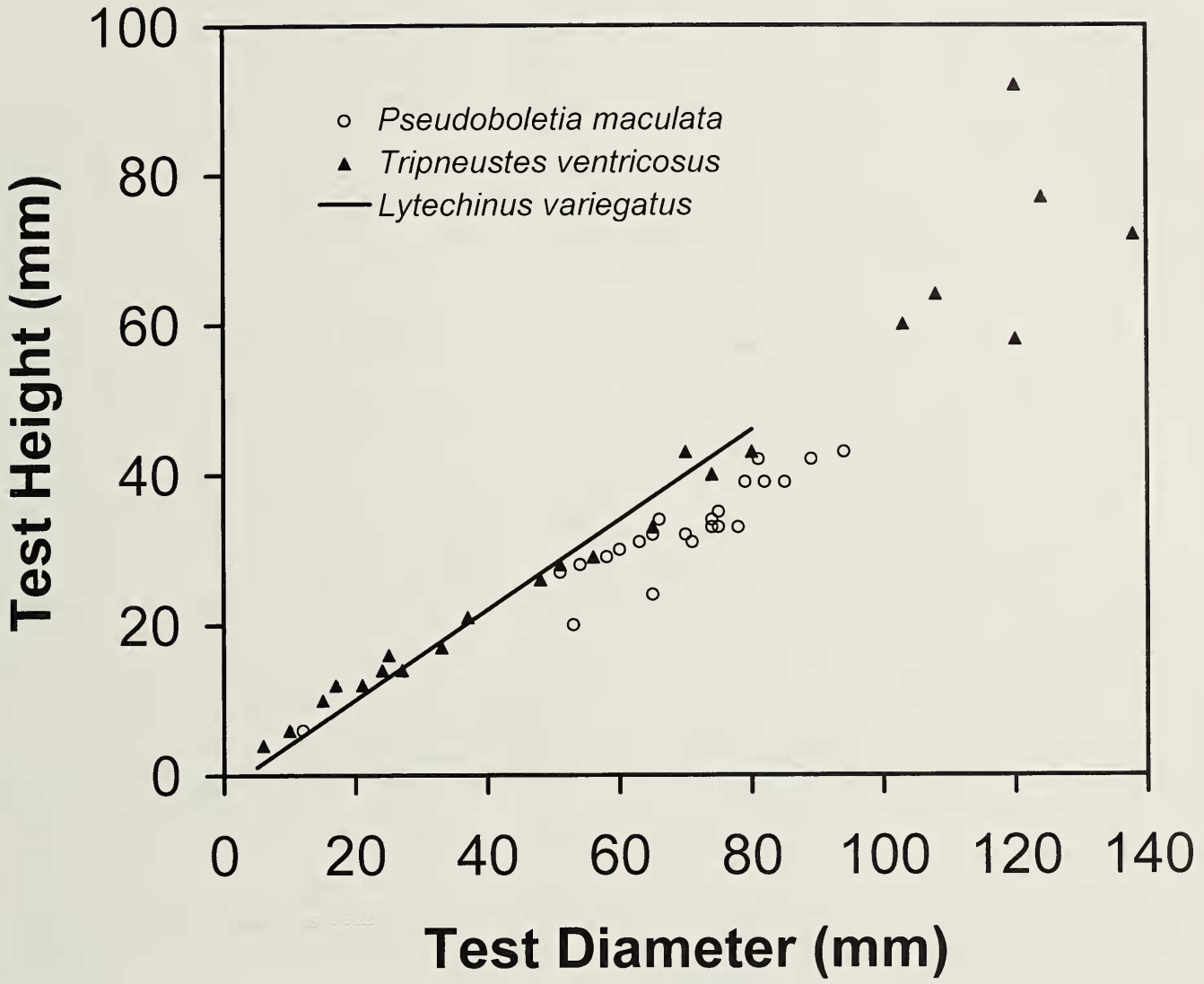

Fig. 4. Test dimensions for three species of toxopneustid echinoid. Data for *Pseudoboletia maculata* are from our material examined, Clark (1925), and Koehler (1908). Data for *Tripneustes ventricosus* are from Mortensen (1943). The line plots Serafy's (1979) equation for *Lytechinus variegatus* using test diameters of his smallest and largest specimens.

a "nodule-covered bottom" at 59 m depth (Texas A&M University 1981). Many of the sea urchins in the photograph held debris on their tests, and spines of most were in contact with those of neighboring urchins. Based on test diameter (51 mm) of specimen TAMU 3-1809, the density of the aggregation was up to 300 m^{-2}. Maculae were not visible on *P. maculata* in the photograph nor on the specimen at hand.

Although the presence of maculae is not a reliable character in *Pseudoboletia maculata* from the Atlantic Ocean (Mortensen 1943, Pawson 1978), other characters readily distinguish this species from other common toxopneustids, viz., *Lytechinus variegatus* and *Tripneustes ventricosus*. The test has a low, hemispherical, subpentagonal shape, with the ratio of test height (TH) to test diameter (TD) generally <0.50 (Fig. 4) in contrast to the higher dome-shaped test of *L. variegatus* (Serafy 1979) and even more depressed than the test of the similar *T. ventricosus*, at least in the range TD = 50–90 mm. *Pseudoboletia* is the only toxopneustid genus bearing spinelets on the buccal plates and other ossicles of the buccal membrane (Fig. 3C); Mortensen (1943) described this condition as a "bearded appearance." The compound plates of the ambulacral series are trigeminate (three porepairs) in *Lytechinus* and *Tripneustes* and

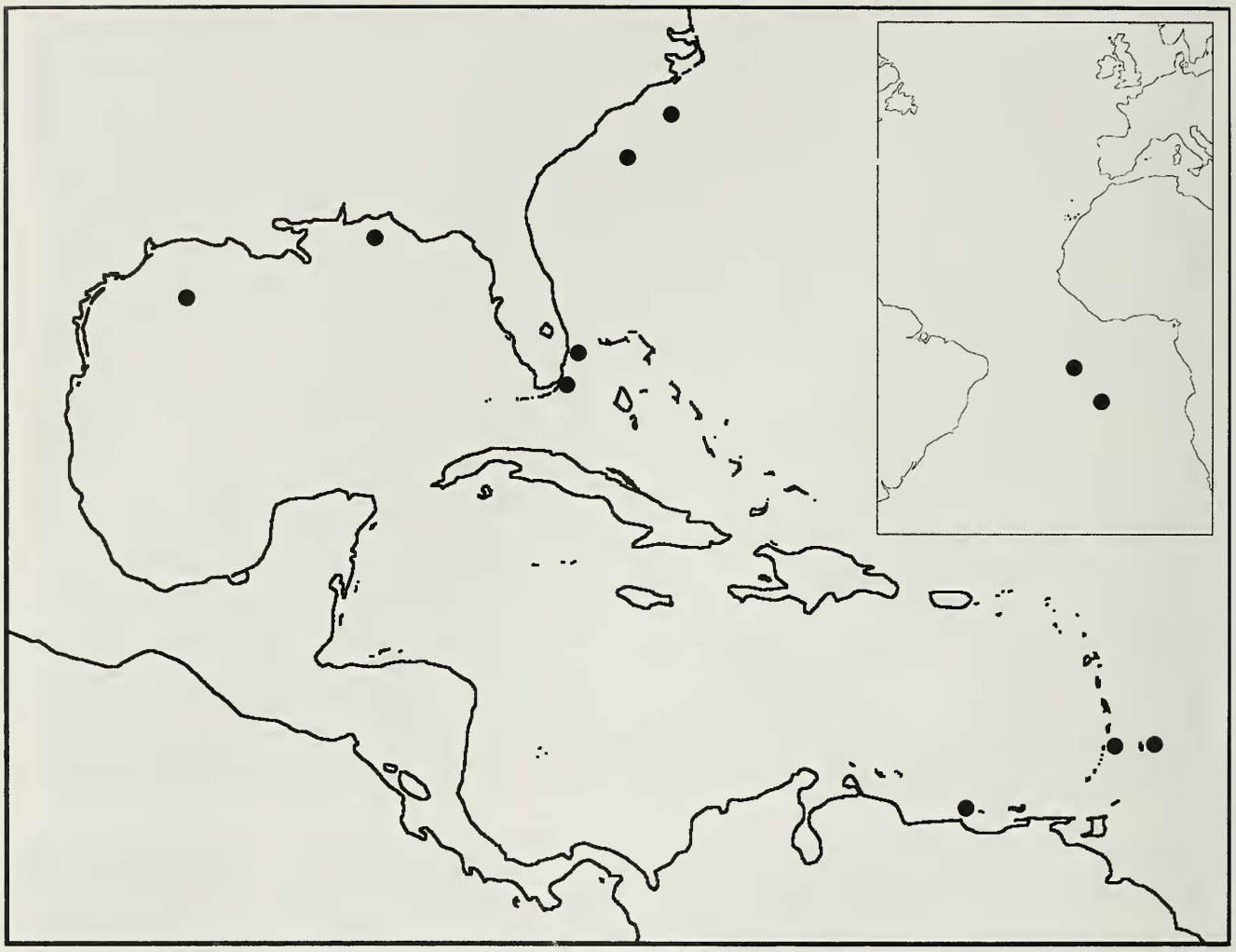

Fig. 5. Distribution of *Pseudoboletia maculata* in the Atlantic Ocean and adjacent waters based on museum records and literature. Each plot might represent multiple nearby records. Inset shows records for Ascension Island and St Helena in the South Atlantic Ocean.

polyporous (four or five pore pairs) in *Pseudoboletia* (Fig. 3C); and the compound plates bear one primary tubercle and spine each in *Lytechinus* and *Pseudoboletia* but one primary spine only every three or four compound plates in *Tripneustes* (Mortensen 1943, Serafy 1979).

Remarks.—Pseudoboletia maculata (s.s.) has a far broader distribution (Fig. 5) than does *Calocidaris micans* (Fig. 2) and is almost pantropical, absent only from the eastern tropical Pacific Ocean. Mortensen (1943) recognized four species of *Pseudoboletia*: *P. atlantica* Clark, 1912 (S Atlantic Ocean), *P. indiana* (Michelin, 1862) (Madagascar to Hawaii), *P. maculata* Troschel, 1869 (Ceylon to Philippines), *P. occidentalis* Clark, 1921 (West Indies). Pawson (1978) included all Atlantic specimens in *P. maculata,* designated *P. occidentalis* as a junior synonym, and recognized two subspecies based on the number of pore pairs in each ambulacral arc: *P. maculata atlantica* Clark, 1912 (five pore pairs, S Atlantic), *P. maculata maculata* Troschel, 1869 (four pore pairs, West Indies). More recently, Liao & Clark (1995) synonymized *P. maculata* with *P. indiana,* effectively rendering *Pseudoboletia* monotypic; but they did not address the taxonomy of the genus in the Atlantic basin, and others (Rowe & Gates 1995, Lane et al. 2000, Liao 2001) have retained the distinction between species. For their lack of comprehensive treatment, we reject the synonymy of Liao & Clark (1995) and tentatively adopt that of Pawson (1978), assigning material from the Gulf of Mexico to *P. maculata*

maculata because of the presence of four pore pairs per arc (Fig. 3C). The genus must, however, be re-evaluated, particularly with the application of molecular techniques, some of which have already been applied to animals from the western Pacific Ocean (Matsuoka 1985, 1986, 1987; Yoshino et al. 1989).

Pseudoboletia maculata has long been known from the Indian and Pacific oceans (Mortensen 1943), sometimes in communities with other grazing echinoids (Shimabukuro 1991). The earliest possible specimens from the Atlantic Ocean might have been taken prior to 1875 by J. C. Melliss off St. Helena (Mortensen 1933), but the first definite record was Koehler's (1908) two specimens taken by R/V *Scotia* in 1904 off Ascension Island at 40 fm [73 m]. Koehler's (1908) description of the two specimens formed the basis for Clark's (1912) new species *P. atlantica.* [A specimen collected by E. W. Alexander off St. Helena is designated by museum records as "holotype" of *P. atlantica* H. L. Clark, 1912 (BMNH 1949.1.18.3). It has a label signed by H. L. Clark and dated "1924," but the meaning of the date is unclear. Clark (1925) described the specimen but did not list it among the 111 echinoid types in the British Museum (Natural History).] A second possible discovery at St. Helena was by J. T. Cunningham in 1909 (Mortensen 1933), mistaken for *Tripneustes ventricosus* (reported as *T. esculentus*) perhaps because of the low, hemispherical, subpentagonal test bearing fine, short spines. Mortensen (1933, 1943) collected at least 12 *P. maculata atlantica* off St. Helena in 1930 "in patches in great numbers" from a depth of 20 m (Mortensen 1933:467; tags written in Mortensen's own hand read "20 m" for USNM E5953 but "50 m" for MCZ 7583) on a bottom of small stones, *Lithothamnion,* and "loose *Furcellaria*-like algae," with which the urchins covered their tests. In 1968–1969, A. Loveridge took additional specimens from St. Helena (USNM E11732, E16096).

Pseudoboletia was first collected in the West Indies in 1918 by C. C. Nutting during the Barbados-Antigua Expedition (Fig. 5). The single specimen (USNM E4531), taken off Barbados "in all probability" from 30–100 fm [55–183 m], is the holotype of Clark's (1921) *P. occidentalis* [but not listed by Downey (1968)], which Pawson (1978) synonymized with *P. maculata maculata.* Clark (1921:117) hailed this specimen as "certainly one of the most noteworthy results of the Barbados-Antigua Expedition," and he expressed surprise that the species had not been taken in earlier expeditions. Additional records include two more specimens from Barbados collected at 12 m (the shallowest Atlantic record) by M. Telford in 1976 (USNM E16246) and one near St. Vincent in 1969 by R/V *Pillsbury* (USNM E20593). Four specimens from the Caribbean Sea collected in 1968 off Venezuela by R/V *Pillsbury* (USNM E12353) were listed by Pawson (1978), along with records off the SE coast of Florida, U.S.A., (USNM E16202, E16203, E16204) in 1974 at 20–21 m. An additional unpublished specimen from Key Largo, Florida, was taken in 1979 on an algal bottom at 51 m (HBOM 72:252). In 1978—the same year in which the first specimens were found in the Gulf of Mexico—three specimens were collected off the coast of South Carolina, U.S.A., at 53–55 m (HBOM 72:278, 72:867); and in 1981, at least 21 specimens were collected in 12 of 24 trawl samples off North Carolina, U.S.A., at depths of 63–102 m (USNM E29626, E29871, E30528, E32267; at least 10 in collection of W. W. Kirby-Smith, in litt.), representing the northernmost Atlantic records to date. The North Carolinian *P. maculata* inhabited "'live bottom' rock outcrops with scattered sand in between" (W. W. Kirby-Smith, in litt.; Duke University Marine Laboratory 1982). The community was dominated in biomass by echinoderms, which clustered at a high level ($\geq$0.7) of constancy along with sponges and decapod crustaceans. Crustose corallines were the only algae reported from the station, and a ridge-

trough system at 100 m depth included rubble with large "lithothamnion balls" (Duke University Marine Laboratory 1982). It is surprising that Project SEAMAP (National Marine Fisheries Service & Florida Department of Natural Resources) took no *P. maculata* in 1983–1985 and 1987 from its 450 trawl and dredge stations at 11–549 m between Stuart (27°10′N) and Fernandina Beach (30°42′N), Florida (R. L. Turner, unpubl.).

Discussion

These records of *Calocidaris micans* and *Pseudoboletia maculata* bring the echinoid fauna of the Gulf of Mexico to 61 species (Table 1), add 2 West Indian-Caribbean species to its fauna, and further reduce its level of echinoid endemism. Of the 47 species that inhabit the continental shelf (0–200 m), 39 species (83%) have West Indian-Caribbean distributions. Serafy (1979) recorded *C. micans, Cidaris rugosa,* and *Stereocidaris ingolfiana* as slope species, but *Calocidaris micans* occurs at 100–144 m in the Gulf of Mexico and *Cidaris rugosa* at 46 m (Barbosa-Ledesma et al. 2000); although Barbosa-Ledesma et al. (2000) did not report the depth for their *S. ingolfiana,* their station coordinates plot well within the 100-m isobath on the continental shelf north of the Yucatan Peninsula. Serafy (1979) considered *Brissopsis alta* to be the only echinoid endemic to the Gulf of Mexico. Since his work was published, *B. alta* has been collected at 12 stations sampled by R/V *Delaware II* and R/V *Chapman* during Project SEAMAP in 1984–1987 between 27°49′N (off Sebastian Inlet, Florida) and 30°20′N (off Jacksonville, Florida) at depths of 177–411 m in the Atlantic Ocean (R. L. Turner, unpubl.). But the addition of *Mellita tenuis,* restricted to the eastern Gulf of Mexico (Harold & Telford 1990), retains the level of endemism at 1 species out of 61 (<2%). Cutress (1980) considered *Calocidaris* to be the only cidaroid genus, Recent or fossil, endemic to the Caribbean Sea; but our records of *C. micans* from the Gulf of Mexico and the Bahamas eliminate the endemic standing of the genus.

We believe that the new records do not represent range extensions but rather increased sampling effort using recent technology (SCUBA, submersibles, ROVs, camera sleds), in some cases in high-relief live-bottom biotopes that were avoided by earlier naturalists, except for the occasional use of rock dredges. This thought parallels those of Hendler & Miller (1984) and Hendler & Turner (1987) for four new species of deep-reef ophiuroids from the Caribbean Sea and Gulf of Mexico. Clark (1921:118) in the description of his new *Pseudoboletia occidentalis* remarked, "It is strange that neither the 'Blake,' the 'Hassler,' nor the 'Albatross,' nor any other collector in the West Indies, has met with the genus but the reason may be that the vessels mentioned did nearly all their collecting outside the 100 fms. line while the other collectors have done very little dredging at any depth. The teeming area between 10 and 100 fms. has scarcely been touched as yet."

Cutress (1980) postulated the extinction of many genera of cidaroid from the Caribbean after the Cretaceous due to lowered salinity, reduced temperature, and heavy sedimentation from terrigenous sources. These conditions might have prevailed also in the Gulf of Mexico more recently during the Wisconsin Glacial Epoch of 100,000–14,000 B.P. (reduced temperature) and with the subsequent postglacial flow of meltwater from the Laurentide ice sheet via Lake Agassiz down the Mississippi River basin in the last 14,000 yr (reduced temperature and salinity, heavy sedimentation, altered surface currents; Broeker et al. 1989, Pielou 1991, Gore 1992, Williams et al. 1998). Only in the last 9000 yr might Caribbean echinoids have invaded the Gulf of Mexico to inhabit new biotopes of the recently flooded continental shelf. Live-bottom echinoids such as *Calocidaris micans* and *Pseudoboletia maculata* would have found suitable habitat only in patches of high relief

Table 1.—Echinoids of the Gulf of Mexico, modified from Serafy (1979). Taxa marked with an asterisk (*) are additions to Serafy (1979). Species in Serafy's (1979) list that remain peripheral are excluded. Geographic distribution beyond the Gulf of Mexico: AA, amphiatlantic; BH, Bahamas; CA, Caribbean and Antillean; ET, eurythermal temperate (Cape Cod south); FK, Florida Keys & SE Florida; MT, Mediterranean; NA, N Atlantic; PT, pantropical; SA, S Atlantic; WA, W Atlantic; WT, warm temperate (Cape Hatteras south).

Taxon	Distribution		Additional sources
	Bathymetric (m)	Geographic	
Order Cidaroida			
Family Cidaridae			
*Cidaris abyssicola**	36–800	CA ET FK	Phelan (1970), Serafy & Fell (1985) Barbosa-Ledesma et al. (2000)
*Cidaris rugosa**	46–790	CA FK WT	Phelan (1970) Barbosa-Ledesma et al. (2000)
*Calocidaris micans**	100–624	BH CA	Present study
Eucidaris tribuloides tribuloides	0–800	BH CA FK SA WT	
*Stereocidaris ingolfiana**	100–1750	AA CA FK	Phelan (1970) Barbosa-Ledesma et al. (2000)
Stylocidaris affinis	23–1000	AA BH CA FK MT WT	
*Tretocidaris bartletti**	48–625	CA FK	Phelan (1970), Hopkins et al. (1991)
Order Echinothuroida			
Family Echinothuridae			
Araeosoma belli	130–1020	CA FK	
Araeosoma fenestratum	160–1180	AA CA FK WT	Mortensen (1935), Serafy & Fell (1985)
Hygrosoma petersii	200–3700	AA CA ET FK	Mortensen (1935)
Phormosoma placenta			
P. placenta placenta	50–3700	AA	Mortensen (1935)
P. placenta sigsbei	200–1800	CA WA	Mortensen (1935)
Order Diadematoida			
Family Diadematidae			
Diadema antillarum	0–400	AA BH CA FK SA WT	
Astropyga magnifica	11–88	CA FK WT	
Centrostephanus longispinus rubicingulus	33–310	CA FK SA WT	Pawson & Miller (1983)
Family Aspidodiadematidae			
Plesiodiadema antillarum	720–3000	AA CA FK SA WT	Mortensen (1940), Serafy & Fell (1985)
Order Salenioida			
Family Saleniidae			
Salenia goesiana	90–540	CA FK	

Table 1.—Continued.

Taxon	Distribution		Additional sources
	Bathymetric (m)	Geographic	
Order Arbacioida			
Family Arbaciidae			
Arbacia punctulata	0–225	BH CA ET FK	
Coelopleurus floridanus	65–2380	CA ET FK SA	Pawson (1978), Serafy & Fell (1985)
Podocidaris sculpta	230–730	CA FK	
Order Temnopleuroida			
Family Temnopleuridae			
Genocidaris maculata	12–420	AA CA ET FK MT	
Family Toxopneustidae			
Lytechinus euerces	55–777	CA FK WT	
Lytechinus variegatus			
L. variegatus carolinus	0–75	BH FK WT	
L. variegatus variegatus	0–250	BH CA FK SA	
Lytechinus williamsi	5–92	CA FK	Hendler et al. (1995)
*Pseudoboletia maculata maculata**	12–155	CA FK PT SA WT	Pawson (1978), present study
Tripneustes ventricosus	0–55	AA CA FK SA WT	Hendler et al. (1995)
Order Echinoida			
Family Echinometridae			
Echinometra lucunter lucunter	0–45	AA CA FK SA WT	Hendler et al. (1995)
Echinometra viridis	0–40	CA FK	Hulings (1955)
Order Holectypoida			
Family Echinoneidae			
Echinoneus cyclostomus	5–570	CA FK PT SA	Pawson (1978)
Order Clypeasteroida			
Family Clypeasteridae			
Clypeaster chesheri	20–101	CA FK	
Clypeaster prostratus	15–75	CA FK WT	
Clypeaster ravenelii	50–230	CA FK WT	
Clypeaster rosaceus	0–285	CA FK WT	Hendler et al. (1995)
Clypeaster subdepressus	5–210	CA FK SA WT	

Table 1.—Continued.

Taxon	Distribution		Additional sources
	Bathymetric (m)	Geographic	
Family Fibulariidae			
Echinocyamus grandiporus	150–2500	AA CA FK	Mortensen (1948)
Family Mellitidae			
Mellita quinquiesperforata	0–180	CA SA	Harold & Telford (1990)
*Mellita tenuis**	0–3		Harold & Telford (1990)
Leodia sexiesperforata	0–60	CA FK WT	
Encope aberrans	12–90	BH FK WT	
Encope michelini	3–90	FK WT	
Order Cassiduloida			
Family Echinolampadidae			
Echinolampas depressa	37–310	CA FK	
Conolampas sigsbei	130–800	CA FK	
Order Spatangoida			
Family Hemiasteridae			
Hemiaster expergitus	380–4833	AA CA FK NA	Mortensen (1950)
Sarsiaster griegii	1900–3120	FK NA	Kier & Lawson (1978)
Family Schizasteridae			
Schizaster orbignyanus	26–500	BH CA ET FK	
Agassizia excentrica	43–900	CA FK	
Hypselaster brachypetalus	750–1750	CA	Mortensen (1951)
Hypselaster limicolus	30–340	CA	
Moira atropos	0–445	CA FK SA WT	
Family Aeropsidae			
Aceste bellidifera	550–5220	AA CA FK NA SA	Mortensen (1950)
Family Brissidae			
Brissus unicolor	0–240	AA CA FK MT SA	Pawson (1978), Hendler et al. (1995)
Brissopsis alta	45–310	FK	Chesher (1968)
Brissopsis atlantica	26–641	BH CA FK	Chesher (1968)
Brissopsis elongata elongata(?)	3–270	CA	
Meoma ventricosa ventricosa	2–200	BH CA FK	Hendler et al. (1995)
Plagiobrissus grandis	1–210	BH CA FK SA	
Plethotaenia spatangoides	150–619	BH CA ET FK	Chesher (1968)

Table 1.—Continued.

Taxon	Distribution		Additional sources
	Bathymetric (m)	Geographic	
Family Loveniidae			
Echinocardium laevigaster	40–220	FK WT	
Homolampas fragilis	360–3550	CA FK	
Family Asterostomatidae			
Archaeopneustes hystrix	38–1610	CA FK	Mortensen (1950)
Palaeobrissus hilgardi	150–1025	CA FK	
Paleopneustes cristatus	76–805	CA FK	

and other locations less prone to sediment accumulation. These events might be factors that explain the strong Caribbean influence and low endemism of the Gulf of Mexico echinoid fauna.

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